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CITATION:

Tsuji, Yamato ...[et al]. Multi-annual variation in the diet composition and frugivory of the Japanese marten (Martes melampus) in western Tokyo, central Japan. Acta Theriologica 2014, 59(3): 479-483

ISSUE DATE:

2014-07

URL:

http://hdl.handle.net/2433/199598

Multi-annual variation in the diet composition and frugivory of the Japanese marten (*Martes melampus*) in western Tokyo, central Japan

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Running headline: multi-annual variation in diet of Japanese martens

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Abstract To examine multi-annual variations in the food habits of the Japanese marten (*Martes melampus*), we analyzed the composition of marten feces in the Bonbori Forest Path in western Tokyo, central Japan in two time periods a decade apart (1997–1998 and 2007–2008). The staple foods of martens in both periods were fruits/seeds and animal materials (mainly insects and mammals). The martens fed frequently on fruits/seeds and insects throughout the year in both periods, but the consumption of mammals, birds, and arthropods/other animals showed seasonal variations. The composition of fruits/seeds and the frequency of occurrence for each fruit-bearing species differed between the two periods. These results suggest that both the foraging strategy and role of martens as a seed dispersal agent changes yearly, presumably according to multi-annual variation in the availability of

prey animals and/or fruits. We emphasize the importance of multi-annual studies both on food habits and to monitor food availability in the temperate region where the food environment changes among seasons as well as years.

Keywords Dietary composition • Frequency of occurrence • *Martes melampus* • Multi-annual • Seed dispersal • Yearly variation

Introduction

Food habit analysis is a basic and important subject in studies on wildlife ecology. The food environment varies both temporally and spatially in accordance with variations in food availability (Herrera et al. 1998; McShea 2000). In temperate regions, marked seasonal changes in plant phenology limit the fruiting period of frugivores (Hanya et al. 2013). Such variations in plant availability often affect the population size of prey animals, such as small rodents and sedentary birds, which in turn affect the food environments of omnivorous mammals (Helldin 1999; McShea 2000). As a result, both frugivorous and carnivorous mammals in temperate regions seem to change their food habits according to environmental conditions (O'Donoghue et al. 1998; Naves et al. 2006; Tsuji et al. 2006; Koike 2010), which implies that multi-annual information on the food habits of animals is needed to fully understand temporal variation in their feeding ecology.

Mustelids (family Mustelidae) are small- to medium-sized mesopredators that have a wide distribution in the Northern Hemisphere (Buskirk et al. 1994). Martens, as generalist predators, switch to alternative prey when their principal foods are not readily available. Several multi-annual studies have shown that martens fed on rodents (voles and mice) during years when their availability was high, while the martens switched to feeding primarily on alternative diets, such as animal carcasses and fruits when the rodent availability was low (Pulliainen and Ollinmäki 1996; Ben-David et al. 1997). These examples imply that information about marten food habits based on short-term studies can lead to erroneous conclusions about their foraging strategies. Mustelids also feed on fruits (Rosalino and Santos-Reis 2009), and therefore potentially disperse intact seeds that pass through their digestive tracts (endozoochory; Wilson 1993; Otani 2002). Thus, multi-annual variation in their food habits can also affect their roles as seed dispersal agents. Despite numerous studies on the food habits of mustelids, few have attempted multi-annual studies on variations in diet composition and its implications.

In this study, we tried to address multi-annual variation in the food habits of wild Japanese martens (*Martes melampus*), an endemic mustelid species in Japan. We especially focused on multi-annual variation in their frugivory. Although several studies have examined the food habits of Japanese martens (Yamagishi 1990; Tatara and Doi 1994; Arai et al. 2003), no study except Arai et al. (2003) documented multi-annual variation. In western Tokyo, the food habits of Japanese marten were previously studied by Nakamura et al. (2001) in 1997–1998 (Period 1 hereafter), and thus we were able to examine

multi-annual variation in diets by conducting a follow-up study in 2007–2008 (Period 2) and comparing the results between these two periods.

Materials and methods

Our study was conducted at the Bonbori Forest Path (36º N, 139º E) between Hachioji City and Akiruno City, approximately 50 km west of the central part of Tokyo. The path is about 10 km long and about 5 m wide, and it is almost entirely asphalt-paved (Tsuji et al. 2011a). Mean annual precipitation and temperature at Hachioji, the nearest weather station to the study site, during Period 1 were 2358 mm and 14.8°C, respectively, while in Period 2, they were 2074 mm and 14.6°C, respectively (Japan Meteorological Agency, http://www.jma.go.jp/jma/index.html). The area is mostly covered with forest vegetation dominated by deciduous broad-leaved secondary forests on slopes as well as planted coniferous forests of *Cryptomeria japonica* and *Chamaecyparis obtusa* in valleys (Nakamura et al. 2001; Tsuji et al. 2011a).

We surveyed the forest path at least once a month from July 2007 to July 2008 (23 surveys in total), and collected marten feces along/on it. When we found feces in one large pile, we treated it as one sample if the color was the same or as independent samples if the color differed. We could easily distinguish marten feces from that of sympatric mammals, such as Japanese macaques (*Macaca fuscata*) and red fox (*Vulpes vulpes*) by its shape. We could also distinguish marten feces from that of sympatric mustelids,

Japanese weasels (*Mustela itatsi*), by its size (mean ± SD width: 10.1 ± 1.5 mm for martens and 6.5 ± 1.1 mm for weasels; Tsuji et al. 2011b). When we collected feces, we removed stones and leaves that were present on the surface.

In the laboratory, defrosted feces were washed through a 0.5-mm mesh sieve, and remnants on the sieve were identified under a microscope. Based on Nakamura et al. (2001), we classified the contents into the following eight categories: mammals (including rodents and insectivores), birds, reptiles/amphibians, insects, arthropods/other animals, fruits/seeds, other plant parts (including leaves, stems, and roots), and others/unidentified items. To examine multi-annual variation in the contribution of fruits, fruits/seeds were sorted to the level of species or genus. Fruits/seeds identification followed Nakayama et al. (2000) and our own references. The percent frequency of occurrence in feces (*%FO* = number of fecal samples containing a specific food item/total number of fecal samples) was used to show seasonal and year-round food habits, as well as multi-annual variation.

We separated the study period into four seasons: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). To test effect of season on the *%FO* of the given food item in each period, we used chi-square tests for independence. If significant seasonal difference was obtained, we conducted *post-hoc* Bonferroni tests to address when the martens fed on the item more frequently. To test the effect of study period on the *%FO* of a given food item in a given season, we used chi-square tests for independence. In these analysis, α was set at 0.05 except for the

Bonferroni tests in which we adjusted the significance levels (α) to 0.013 (for 4 seasons) and 0.017 (for 3 seasons) to avoid type I error. Data analyses in this study were performed using the statistical software R 2.15.1.

Results

During Period 2, we collected 381 fecal samples, among which we analyzed 257 samples (N = 33 in spring, 20 in summer, 26 in fall, and 178 in winter). In total, 594 identifiable food items were found in the 257 fecal samples, which corresponded to an average of 2.32 food categories per fecal sample (SD = 0.83, range: 1–5). Fruits/seeds (annual *%FO*: 94.9), mammals (annual *%FO*: 69.6), insects (annual *%FO*: 51.0), and other plant parts (annual *%FO*: 61.5) were the staple food items during Period 2 (Table 1). Birds, reptiles/amphibians, arthropods/other animals, and fungi were supplementary sources, whose annual *%FO*s were less than 5%.

As to seasonal change, the *%FO* of mammals in Period 2 was significantly higher in spring and summer than winter ($p < 0.017$). The *%FO* of birds in Period 2 was significantly higher in spring than winter ($p < 0.013$). The *%FO* of arthropods/other animals in Period 1 was significantly higher in spring than other seasons ($p < 0.013$), while *%FO* of arthropods/other animals in Period 2 was significantly higher in summer than winter ($p < 0.013$) (Table 1).

Significant effects of study period on *%FO* were detected for mammals in the annual mean (χ^2 =

4.7, $df = 1$, $p = 0.031$) , for birds in winter ($\chi^2 = 11.8$, $df = 1$, $p < 0.001$), reptiles and amphibians in the annual mean ($\chi^2 = 3.9$, $df = 1$, $p = 0.049$), arthropods/other animals in the annual mean ($\chi^2 = 11.1$, $df = 1$, $p < 0.001$), and other plant parts in each season (spring: $\chi^2 = 16.3$, $df = 1$, $p < 0.001$; summer: $\chi^2 = 20.0$, $df = 1$, $p < 0.001$; fall: $\chi^2 = 11.4$, $df = 1$, $p < 0.001$; winter: $\chi^2 = 9.3$, $df = 1$, $p = 0.002$; the annual mean: $\chi^2 = 65.1$, $df = 1$, $p < 0.001$). However, no significant difference in *%FO* was observed for insects and fruits/seeds among the study periods ($p > 0.05$ for each; Table 1).

Throughout the study periods, at least 19 species of fruits/seeds were found in the feces. Some fruits appeared in feces during only one period (Table 1): in spring, *Rubus* spp. and *Aspidistra elatior* fruits appeared only in Period 1, while *Actinidia arguta*, *Stachyurus praecox*, *Morus bombycis*, *Hovenia dulcis*, *Pyrus pyrifolia*, *Celtis sinensis*, *Aphananthe aspera*, and *Physalis alkekengi* appeared only in Period 2; in summer, *Rubus* spp., *A. arguta*, and *Broussonetia kazinoki* appeared only in Period 1, while *M. bombycis* appeared only in Period 2; in fall, *Rubus* sp., *H. dulcis*, and *Cinnamomum camphora* appeared only in Period 1, while *C. sinensis*, *Viburnum dilatatum*, *Cocculus orbiculatus*, and *Sorbus* sp. appeared only in Period 2; in winter, *Cardiospermum halicacabum*, *Mollugo verticillata*, and *Prunus* sp. appeared only in Period 1, while *S. praecox*, *H. dulcis*, *P. pyrifolia*, *C. sinensis*, *Prunus jamasakura*, *Actinidia polygama*, and *Vitex* spp. appeared only in Period 2 (Table 1).

Variation in *%FO* was also observed in several fruits between the two periods. In fall, the *%FO* of *A. arguta* was significantly higher during Period 2 ($\chi^2 = 3.9$, $df = 1$, $p = 0.049$). In winter, the *%FO*s of

Rubus spp. (χ^2 = 4.7, *df* = 1, *p* = 0.030) and *Diospyros kaki* (χ^2 = 51.2, *df* = 1, *p* < 0.001) were significantly higher in Period 1, while the *%FO* of *A. arguta* (χ^2 = 10.1, *df* = 1, *p* = 0.002) was higher in Period 2. On an annual basis, the *%FO*s of *Rubus* spp. (χ^2 = 14.9, *df* = 1, *p* < 0.001), *D. kaki* (χ^2 = 11.2, *df* = 1, *p* = 0.001), *Akebia quinata* (χ^2 = 14.1, *df* = 1, *p* < 0.001), and *P. jamasakura* (χ^2 = 15.7, *df* = 1, *p* < 0.001) were significantly higher in Period 1, while those of *A. arguta* (χ^2 = 45.5, *df* = 1, *p* < 0.001) and *S. praecox* (χ^2 = 8.5, *df* = 1, *p* = 0.003) were significantly higher in Period 2 (Table 1).

Discussion

Japanese martens in the Bonbori Forest Path fed mainly on animal materials and fruits during both study periods. Their omnivorous diets were similar to what has been reported at other sites (Yamagishi 1990; Tatara and Doi 1994; Arai et al. 2003). In terms of seasonal changes in food habits, the martens fed frequently on fruits/seeds and insects throughout the year in both periods, while other categories, like mammals, showed seasonal variation.

We found variation in dietary composition between the two study periods: the annual *%FO*s of mammals, reptiles/amphibians, and arthropods/other animals were higher, while those of some berry species were lower in Period 1 than in Period 2. Since climatic conditions were similar between the two periods (see Materials and methods), the results strongly suggest three possibilities: fruit production varied annually, prey animal abundance varied annually, or both fruit production and prey animal

abundance varied annually. The availability of prey animals (Saito et al. 1998, 2007) and fruit production (Komiyama et al. 1991; Suzuki et al. 2005) are known to vary annually in Japan. Thus, the martens at our study site seem to adjust their dependence on animal materials in accordance with the availability of prey animals and/or fruits, as do other mustelids (Buskirk et al. 1994; Pulliainen and Ollinmäki 1996; Zhou et al. 2011; Caryl et al. 2012). In this study we could not quantify the food availability, and our interpretation of the multi-yearly variation in the dietary composition is speculative. Collecting such information would be useful to investigate how dietary preferences change with availability of their staple foods.

We also found considerable variation in fruit occupation in the fecal composition between the two study periods. A similar phenomenon was noted by Otani (2002) when studying martens in northern Japan: he found differences in fruit composition among samples during a 2-year study; e.g., seeds of *Taxus cuspidata* var. *nana* and *Prunus nipponica* were only found in feces in 1 year. These results can be attributed to yearly variation in fruit production. In our study, for example, the availability of *A. arguta* and *S. praecox* from fall to the next spring should have been greater in Period 2, while the availability of *Rubus* sp. in all seasons except for fall, *D. kaki* and *A. quinata* in fall, and *Prunus japonica* in summer should have been greater in Period 1. This implies that the role of Japanese martens as seed dispersal agents would also vary annually according to fruit availability.

The annual *%FO* of other plant parts, mainly leaves, was higher in Period 2. Because we removed

leaves that were attached to the surface of fecal samples at collection, detected leaves were likely to be food-originated. Folivory by Japanese martens has been reported at other study sites (e.g., Shiratsuki et al. 1973; Yamagishi 1990). Whether folivory is a "side effect" of capturing insects on leaves or a separate feeding strategy of the martens is not clear. The amount of leaves in feces, however, was very low (Yamagishi 1990), and the relative importance of leaves for martens seems lower than that of fruits and animal matter.

We demonstrated that multi-annual studies are required to fully understand temporal variation in marten diet. Furthermore, monitoring the availability of plant and prey animals is necessary to explain multi-annual variation in the foraging behaviors performed by martens (e.g., Pulliainen and Ollinmäki 1996; Ben-David et al. 1997; Caryl et al. 2012) and to confirm their role as a seed dispersal agent (Otani 2002; Tsuji et al. 2011a). Accumulating such fundamental data from multiple time points and localities would be useful to meta-analyses investigating large-scale drivers of prey availability and diet.

Acknowledgments This study was supported in part by the Cooperative Research Fund of the Wildlife Research Center, Kyoto University, and Grants-in-Aid from the Department of Academy and Technology of Japan (No. 20255006). We would like to thank handling editor and two anonymous reviewers for their constructive comments on an earlier version of our manuscript.

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Table 1. Seasonal change in food habits of Japanese martens in Bonbori Forest Path, western Tokyo, central Japan based on fecal analyses and expressed as frequency of occurrence (*%FO*) from the feces.

Food Item	Spring (March-May)			Summer (June-August)			Fall (September-November)			Winter (December-February)			Annual			Seasonal Change	
	Period 1	Period 2		Period 1	Period 2		Period 1	Period 2		Period 1	Period 2		Period 1	Period 2		Period 1	Period 2
	N = 40	N = 33		N = 49	N = 20		N = 48	N = 26		N = 31	N = 178		N = 168	N = 257			
Animal materials	85.0	72.7	NS	71.4	90.0	NS	66.7	46.2	NS	45.2	50.6	NS	92.9	69.6	NS	NS	NS
Mammals	42.5	36.4	NS	28.6	30.0	NS	—	—		12.9	6.2	NS	20.8	11.3	*	*** (Sp = Su = Wi)	*** (Su > Wi, Sp > Wi)
Birds	12.5	15.2	NS	2.0	10.0	NS	2.1	3.8	NS	16.1	1.1	***	6.5	3.9	NS	* (Sp = Su = Fa = Wi)	** (Sp > Wi)
Reptiles/amphibians	10.0	—		—	—		6.3	—		—	1.1		4.2	0.8	*	NS	NS
Insects	37.5	48.5	NS	51.0	80.0	NS	64.6	42.3	NS	32.3	49.4	NS	48.8	51.0	NS	NS	NS
Arthropods/other animals	37.5	3.0	NS	6.1	20.0	NS	2.1	—		3.2	1.1	NS	11.9	2.7	***	*** (Sp > Su, Sp > Fa, Sp > Wi)	*** (Su > Wi)
Plants	55.0	97.0	NS	65.3	95.0	NS	97.9	100.0	NS	96.8	100.0	NS	80.0	100.0	NS	NS	NS
Fruits and seeds	52.5	84.8	NS	63.3	70.0	NS	97.9	96.2	NS	96.8	99.4	NS	77.4	94.9	NS	NS	NS
Rubus spp.	17.5	—		14.3	—		2.1	—		12.9	2.2	*	11.3	1.6	***		
Diospyros kaki	7.5	3.0	NS	—	—		2.1	11.5	NS	83.9	6.2	***	17.9	5.8	***		
Akebia quinata	2.5	3.0		—	—		60.4	38.5	NS	3.2	1.7	NS	19.0	5.4	***		
Aspidistra elatior	2.5	—		—	—		—	—		—	—		0.6	—			
Actinidia arguta	—	39.4		8.2	—		33.3	80.8	*	19.4	81.5	**	15.5	69.6	***		
Stachyurus praecox	—	39.4		—	—		14.6	3.8	NS	—	12.9		4.2	14.4	**		
Morus bombycis	—	15.2		—	45.0		—	—		—	—		—	5.4			
Hovenia dulcis	—	6.1		—	—		4.2	—		—	0.6		1.2	1.2	NS		
Pyrus pyrifolia	—	6.1		—	—		—	—		—	1.1		—	1.6			
Celtis sinensis	—	3.0		—	—		—	3.8		—	3.4		—	3.1			
Aphananthe aspera	—	3.0		—	—		—	—		—	—		—	0.4			
Physalis alkekengi	—	3.0		—	—		—	—		—	—		—	0.4			
Prunus jamasakura	—	—		36.7	10.0	NS	—	—		—	0.6		10.7	1.2	***		
Broussonetia kazinoki	—	—		6.1	—		—	—		—	—		1.8	—			
Actinidia polygama	—	—		—	—		6.3	3.8	NS	—	1.1		1.8	1.2	NS		
Cinnamomum camphora	—	—		—	—		2.1	—		—	—		0.6	—			
Viburnum dilatatum	—	—		—	—		—	3.8		—	—		—	0.4			
Cocculus orbiculatus	—	—		—	—		—	3.8		—	—		—	0.4			
Sorbus sp.	—	—		—	—		—	3.8		—	—		—	0.4			
Cardiospermum halicacabum	—	—		—	—		—	—		3.2	—		0.6	—			
Mollugo verticillata	—	—		—	—		—	—		3.2	—		0.6	—			
Prunus spp.	—	—		—	—		—	—		3.2	—		0.6	—			
Vitis spp.	—	—		—	—		—	—		—	1.7		—	1.2			
Nuts	10.0	—		—	—		2.1	—		—	—		3.0	—			
Poaceae	—	3.0		—	—		—	—		—	1.7		—	1.6			
Polygonaceae	—	3.0		—	—		—	—		—	—		—	0.4			
Other seeds	25.0	—		—	—		2.1	—		6.5	—		7.7	—			
Other plants	5.0	75.8	***	4.1	85.0	***	4.2	50.0	***	9.7	57.9	**	5.4	61.5	***	NS	NS
Fungi	2.5	6.1	NS	—	—		—	—		—	2.3		0.6	2.5	NS		
Others/unidentified materials	5.0	6.1	NS	2.0	5.0	NS	6.3	—		—	2.3		3.6	2.5	NS		

Effects of study periods on the *%FO* are also shown for each season (performed by chi-square tests for independence). ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$, NS: not significant ($p > 0.05$)
Results of multiple comparison (Bonferroni tests in which significant leves (α) are adjusted to 0.013 (4 comparisons) and 0.017 (3 comparisons)) are shown in parenthesis
Period 1: 1997-1998 (from Nakamura et al. 2001)
Period 2: 2007-2008

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